The Fertilization of Three Native Plants.*

By E. G. Hill.

I.—*Campanula aparinoides*, Pursh.

It is well known that species of *Campanula* are adapted to cross-fertilization by the agency of insects, the flowers being proterandrous. This was clearly worked out and described by C. Sprengel in his famous book, the pioneer of work in this line, published at Berlin in 1793†. The illustrations in the plates (Taf. 9, 11.) accompanying the letter-press are good representations of what may be seen in species figured there, or in those allied to them. Hermann Müller, in his two principal works on the fertilization of flowers by insects‡, enters into their structure and adaptations with considerable detail, and with careful analysis, giving examples of several species and full illustrations in typical cases. All follow the same general plan, the individual variations being slight, since the species conform to a type more uniformly than genera usually do, as is also the case with the allied genus *Phyteuma*. The whole arrangement is very curious and interesting, being well planned to secure the designated end. *Campanula aparinoides*, Pursh, does not differ in any essential point of structure from the other members of the genus. The nectar, which is the object sought by visiting insects, is stored in a yellowish, fleshy disk, resting on the pistil and surrounding the base of the style. The disk is nearly covered by the enlarged bases of five filaments, termed "valves" by Sprengel, quite triangular in shape in *C. rotundifolia* and some other species, and rather elongated triangular in *C. aparinoides*. The five free spaces between these "valves" or enlarged bases of the filaments, are themselves nearly closed by interlocking hairs, projecting from the edges of the filaments.§ In *C. aparinoides* there are also hairs projecting from the inner side of the corolla at its base, and directed inwards towards the filaments. In the bud, and during the early stages of its development, the anthers, like a hollow

---

* Read before the State Microscopical Society of Illinois, Dec. 12, 1890.

† Das entdeckte Geheimniss der Natur im Bau und in der Befruchtung der Blumen, pp. 109-112.

‡ Die Befruchtung der Blumen durch Insekten, und Alpenblumen.

§ H. Müller, Befruchtung, p. 373.

cylinder, are closely wrapped around the upper part of the style, which is shaped like a hairy, cylindrical brush. The anthers burst along their inner face at this time, and the brush, by means of the bristling hairs, sweeps the pollen out of them pretty cleanly. As they shrivel up and shrink away towards the bottom of the bell-shaped corolla, the style lengthens, bearing the spherical pollen grains with it while the flower is unfolding. The stigmas are still inaccesssible to the pollen, since they form the inner faces of the three-cleft style, the parts of which are closed on one another, and form the cylindrical brush. They soon open and curve backward, exposing their inner surfaces, now turned outward and covered with stigmatic papillæ. As they curve back, they hold the same position in the flowers as did the brush a little earlier. Hence an insect, creeping into the corolla to reach the nectar, rubs off some pollen from the brush of a younger flower and carries it to the stigma of an older one, the parts of the style being curved back in such a way that it cannot, if of any considerable size, avoid brushing off some of the dust and leaving it on the papillose stigmas. In this way, as an insect goes from flower to flower, the ovules of an earlier flower are fertilized by the pollen of a later one.

The older botanists were puzzled to account for the fertilization of these plants. The relative position of the parts was well known to Linnæus and his pupils. In a dissertation by one of them, Wahlbom, entitled, "Sponsalia plantarum," and read at Upsal in 1746, it is stated that certain canals existed in the style to carry the pollen through to the stigmas.* Sprengel remarks that they did not see these canals, but imagined them. It was an effort to bridge a difficulty, and, like many another, broke down when the test was made.

The function of the hairs fringing the bases of the stamens is considered by Müller to be that of keeping useless visitors from the nectar stored in the fleshy disks just within. Strong insects like bees, that are the most common visitors of *Campanulæ*, can push through them and secure the nectar the nectar-disks being covered by them and the "valves." Weak insects will be kept away. Sprengel looked upon them as contrivances to protect the

* Linnæus, Fundamenta Botanica, 1786, Vol. I, p. 246.

nectar from the rain, by preventing the entrance of drops of water, but this is thought to be useless by Müller on account of the inverted position of the flowers, actually causing them to be sought by insects as a shelter from rain and dew, and so facilitating their fertilization by these casual visits. But they would not be useless for this purpose in the case of *C. aparinoides*, whose flowers open upward, they being nearly erect on their slender stems.

There are plenty of guests, bidden or unbidden, in the flowers of the Marsh Bellwort. Nearly every one has a goodly number of Thrips, (*Palæothrips*, Sp.), crawling about in various parts of it, and busy at something. Sprengel states that they were the only insects he had seen in the species of *Campanula* he mentions, five in all including *Specularia*, but he thought that they could hardly affect fertilization, and that this must be done by some larger insects. Among the insects mentioned by Müller, nothing is said of Thrips. But it seems evident that they may be useful in the case of *C. aparinoides* from a study of the flower and its surroundings. These do not, as already intimated, like species with inverted corrollas, offer shelter to the bees and other insects at night or during rain. Though the flowers are white or bluish-white, they are neither conspicuous nor very accessible, since they are usually down among the blades of grass where they most delight to grow. Sometimes they stretch upward and offer inducements of this kind, which may also be both a cause of superior vigor and a result of insect visitation. But the Thrips are the only insect visitors I find at all common. Others are occasionally seen, small butterflies and moths and bee-like flies, and they not alighting very often. When the Thrips are placed upon a slide and examined, they will be seen to be plentifully sprinkled with spherical grains of pollen, adhering to various portions of their bodies, especially to the antennæ and the body-hairs. They crawl around in the base of the flowers, and over the style and stigmas. They appear too small to go from one flower to another to any extent, and especially from one plant to another, though this is not impossible, since the plants sometimes grow so closely together as to be grasped by the hand and pulled up by the handful. But it is not probable that fertilization is effected in this manner to any degree.

But it may be the office of these tiny insects to effect self-fertilization in flowers that do not often receive visits from larger insects, for whose visits they are, however, functionally contrived. They bring about results which, though inferior, are greatly superior to failure of pollenation. Though the flowers are proterandrous, the round and unbroken grains of pollen are still visible on the outer side of the style some time after its parts have expanded and exposed the stigmatic surfaces. The Thrips will be useful in carrying this pollen across to the other side, and in this way overcome a difficulty which the pupil of Linnæus imagined must be obviated by his supposed canals.

Both the ability and desirability of self-fertilization in case of a lack of insect-visitation have been recognized by Müller and other writers as probable in species of *Campanula*.* He indeed calls it a makeshift (möglichkeit), but as such it is far better than failure in accomplishing the development of seed. He mentions *C. barbata*, L., as an example of this kind, where, if cross-fertilization fails, self-fertilization may take place. The method of securing this is for the parts of the style to curve around till their stigmatic faces come in contact with the lower part of the brush formed by the undivided portion of the style, or by the pollen falling on the stigmas when they are in this position. The parts of the style would have to curve into a circle to bring the two sets of hairs, those on the brush and those on the stigma, into this relation. But they do not appear to curve so far in the flowers of *C. aparinoides*. This condition of affairs also implies that the pollen of a flower is available for its own fertilization when the parts of the style expand and long enongh afterward to allow them to curve to make the required contact. And this is corroborated by finding fresh pollen on the brush and on the Thrips, which, though it might have been brought from other flowers, is more likely to have been left for use by their own anthers. And it seems much easier and more satisfactory to make the Thrips

* "The *Campanulaceæ* have been inquired into by many investigators as a supposed case of necessary self-fertilization, some of whom, Cassini, Treviranus, Hartig, and Gaertner, decide for it; others, Sprengel, Wiegman and Henschel, against. According to my investigations, which, however, are to be extended by more exact experiments, self-fertilization does not take place."—Hildebrand, Geschlechter Vertheilung bei den Pflanzen, p. 64, (Leipzig, 1867.)

pollen carriers than for the parts of the style to curve around and gather their own pollen, functionally intended for the use of other flowers. Viewed in this manner they would not be termed useless guests, or be classed among the insects engaged in petty thefts* (Diebstähle) while busily crawling about among the hairs of the Marsh Bellwort, which they do so easily, but among those lawfully employed in proper work.

II.—*Sabbatia angularis*, Pursh.

This handsome member of the Gentian family is a common plant in many of the damp places of our pine barrens, blooming in late summer and early autumn. But its floral beauty is not its sole feature of attraction. The mechanism to secure cross-fertilization by the help of insects is still more interesting. The flowers, like others of the genus, are proterandrous, and skillfully contrived to secure this end. They have a wheel-shaped corolla, rose-pink in color, very bright and attractive to the eye. At the base of its short tube is a yellow or greenish-yellow spot, shaped somewhat like a star with five short, blunt rays, bordered by a dark red or purple band, contrasting sharply with the general color of the flower. The style is bent downward and outward, bringing it to one side of the flower, or away from the floral axis. It is deeply two-cleft; occasionally three-cleft. In the bud the corolla is dextrorsely convolute. The style and its parts share in the same spiral movement seen in the twisting of the bud, it being sinistrorsely twisted. The two parts of the style face each other, their inner surfaces stigmatic for the greater part of their length and thickly covered with glandular hairs. These parts are closed in the bud, and until after the anthers burst. The bending of the style is in a plane parallel with the cleft, or away from which the two parts of the style would recede at a right angle if they were not twisted. This would leave the stigmas with their edges only presented to the body of an insect at work above or below them, unless they spread considerably, so as to allow it to pass through the fork between them, which is not the case. But the twisting, owing to the length of the parts, tends to hold them together, as a cord is twisted to bind its threads better. Yet it

* Müller, Befruchtung der Blumen, p. 373.

compensates in a measure for this by bringing a good part of the stigma to the upper side of the style, so as to rub against the body of an insect trying to reach the nectar in the most advantageous way. For, in looking at a flower from the outside, the twisting is seen to be towards the left hand. The style makes a turn, bringing that part of the fork axially on the right over to the left. Since the cleft extends about half way down, this part of the fork, in the effort to withdraw from the other and turn at the same time, rolls its inner face upward for a good portion of its length, being still held to the opposite part at the upper end; and turning it wholly upward, except at the tip (which may have turned too far for this), in case it is released. By the same process, the part of the fork axially on the left passes over to the right, much of the inner surface being turned downward. Sometimes the tips of the parts in either case may turn so far as to bring the ends of the stigmas upward or downward, and opposite to the position of their main parts respectively. This is a great advantage, by making the larger part of the stigmatic surfaces easily accessible, since the parts of the style diverge but little when they succeed in separating, for the interlocking is often quite strong. The erection of the style, a characteristic of species of *Sabbatia* in later anthesis, is not a prominent feature of *S. angularis*. In fact, when it occurs, it is of no special advantage for cross-fertilization in this plant, the stigmas being well exposed while the style is turned to one side. Fertilization may thus begin at an earlier stage, with fewer chances of failure, should the parts remain locked together. Besides, the style, being quite stiff, when turned to one side offers a better landing-place to a large insect, by affording more room on one side of the corolla of a flower not very broad.

The object of these visits is to get the nectar stored in receptacles attached to the base of the ovary. These project outward and downward as little swellings, each nectary opposite a petal and to a point of the star forming the eye at its base. Hence they alternate with the stamens, which are of the same number as the lobes of the corolla and opposite its clefts. It is between the filaments that an insect would run its proboscis to reach the nectar-glands, the bright line raised up into blunt points exactly

opposite them serving as a guide. The tube of the corolla is about as long as the ovary. The style and ovary are green. The anthers are introrse and adnate, though the point of attachment to the filament is a little above their base, making them slightly versatile, so far at least as to turn back with facility. At the time of bursting they bend back, becoming arcuate in shape and open upward. When an insect lights upon a flower and turns about in the effort to reach the various nectaries, these anthers are favorably situated to leave the pollen on its under side. The stigmas of the flower being closed on one another are not yet in a condition to receive this pollen, except a small quantity which may be left on the few hairs that project from the edges of the cleft. But when an older flower is subsequently visited, it will have its stigmas turned in the proper way for the reception of the grains. Working about the flower to obtain the nectar, all parts of the exposed stigmas are likely to come in contact with some part of the insect to which pollen adheres, and the grandular stigmatic hairs will rub it off and hold it. In this way cross-fertilization will be effectually secured.

The structure and mode of bursting of the anthers is an additional help in this process. By curving they are made stiff, and their walls are stretched. The tissue of the cell-walls is very elastic. While experimenting with the anthers to see how they opened, one was pressed along its sides between the prongs of a pair of forceps. The instrument suddenly slipped, and the shock, or relief from pressure, was so great that the cells burst, quickly throwing out the pollen to quite a distance. Repeating the experiment and imitating the first operation as nearly as possible, others were ruptured in the same manner. Sometimes the elastic force was so great as to nearly empty the cells by a single effort. Doutless an insect will also exert a like pressure, by grasping the anthers with its feet or pressing them between its legs while at work upon the flower, and cause their bursting in a similar way. As a result the pollen will be shot against its body, and more adequately dust it than by a simple act of rubbing against them. The tissues of the cells being stretched and the anthers bent into the form of a bow, as soon as they are unloosed, shoot out their tiny missiles, stored up within, and hit their insect guests, not as enemies, but as agents of the plant in furthering its economy.

III.—*Eleocharis mutata* (L.) R. & S.

This plant was detected during the present season in Wolf Lake, along the eastern border of Chicago, and near the boundry line of Indiana. It grew in abundance but had hitherto escaped the notice of collectors in this vicinity, as I find no allusions to it in this locality. An examination of its flowers showed that they were proterogynous, the protruding style and stigmas being brown and withered while the stamens are still covered by the scales. A further study of the plants showed that the styles appear above the scales just after the spikes have risen out of the water from one to three or four inches. When the plants have stretched upward from six to twelve inches beyond their proterogynous stage, the anthers make their appearance above the scales. The spikes are about an inch in length at first, but increase in length and diameter as they become older, or reach their second stage. Then the anthers burst, and freely scatter the dry pollen about, some of which will lodge on the feathery stigmas. The plant is fertilized by the wind, or even by simple gravity, since the stems are near together, several rising from the same rhizome. The elevation of the spikes when the stamens appear, bringing them above the younger flowers in which the stigmas are ready to receive the pollen, facilitates its reaching them at a level so much below, since it may simply drop upon them. But the wind, either directly or by agitating the water and shaking the stems, must be regarded as the principal agent in the cross-fertilization of the flowers. The inflorescence of the spikes is centrifugal, the older stamens being mostly above. Belated stamens sometimes appear without anthers. They rise above the scales as pale elongations of filaments, a little enlarged at the top.

ENGLEWOOD, CHICAGO.

Variations in the Rootstock of Smilax glauca dependent upon Environment.

On the south beach of Staten Island, at the line of high water, there are often a number of hard, gall-like bodies, lying on the sand. These are sea-worn parts, often single tubers, from the rootstock of the cat-brier, probably in every case from *Smilax glauca*. This species grows on the bluffs that are constantly